TOWARD A PHYLOGENETIC CLASSIFICATION OF THE MYCALIDS WITH ANISOCHELAE (DEMOSPONGIAE: POECILOSCLERIDA), AND COMMENTS ON THE STATUS OF *NAVICULINA* GRAY, 1867

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Phylogenetic relationships for mycalids with anisochelae are revised. Several likely monophyletic species groups are included, currently assigned subgeneric rank or lower, totalling 12 groups, with special reference to *Naviculina*. The type species of *Naviculina*, *N. cliftoni* from SW Australia, is redescribed and its alleged relationship to *Arenochalina mirabilis* is contested, with more suitable affinities to *Aegogropila*. Its main anisochelae are termed here naviculichelae. A preliminary revision of over 230 published species names for *Mycale* and allied taxa with anisochelae was undertaken looking for *N. cliftoni*'s kinship, yielding four likely candidates: *M. cleistochela* (from the W Indian Ocean and Indonesia), *M. diastrophochela* (from the Vema Seamount, SE Atlantic), *M. obscura* (from Indonesia and pan Australia), and *M. peculiaris* (from Papua New Guinea). A phylogeny is proposed for mycalids with anisochelae, although not fully resolved, and alternative phylogenetic classification schemes are hypothesised with discussion on the relative merits of each one.☐ *Porifera, phylogenetic classification, Mycale, Naviculina, phylogeny, Linnean hierarchy.*

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Naviculina was erected by Gray (1867) for Bowerbank's (1864: 252, pl. XXXVII, fig. 152) 'naviculoid spiculum', thought by him to belong to *Hymedesmia*. Gray (1867) was mistaken in calling the spicule 'equibianchorate', since its anisochelate condition was apparent in Bowerbank's illustration. Gray's (1867) concept of Esperiadae, to which he associated *Naviculina*, was essentially based on the possession of sigmas and/or chelae than on any other feature. Despite the excellent state of preservation of the type slide of *N. cliftoni* (Fig. 1), revealing a neat ectosomal reticulation of bundles of mycalostyles, no closer relationship was suggested by Gray (1867) between *Naviculina* or any other mycalid assemblage: *Mycale, Aegogropila, Grapelia* and *Carmia*. Hooper & Wiedenmayer (1994), on the contrary, considered *Arenochalina* Lendenfeld, 1887, a junior synonym of *Naviculina*, thus postulating a closer relationship between both taxa.

It is the purpose of this article to explore the probable relationships of *Naviculina* and *Aegogropila* Gray, 1867 (as inferred from their sharing of a neat ectosomal reticulation), none of which is a synonym of the other in phylogenetic terms. It is postulated that *Arenochalina* deserves status as a valid subgeneric assemblage of *Mycale*, in view of its possession of a choanosomal stout quadrangular reticulation of spiculofibres (cf. Hajdu & Rützler, 1998). Worldwide records of *Mycale* and allied genera are revised and a list of species which are best allocated to *Mycale (Naviculina)* is proposed. Hajdu & Desqueyroux-Faúndez's (1994) cladistic analysis of the Mycalidae is reconsidered, with the inclusion of *Mycale (Naviculina)*, and the likely monophyletic species-groups of *Mycale*.

PHYLOGENETIC TAXONOMY. The need for a phylogenetic taxonomy has been recently stressed by de Queiroz & Gauthier (1992, and references therein), who claim that taxon names will never be explicit, universal and stable, as envisaged by the implementation of the diverse biological codes of nomenclature, if definitions continue to be assembled from lists of characters (but see Wiley, 1979). By accepting that characters may be reduced (lost), it is easily seen that groupings defined on these terms will frequently be artificial (Sundberg & Pleijel, 1994).

The matching of evolution and systematics implies in the equation of species with population lineages, and of higher taxa with clades

(Christoffersen, 1995; Cantino et al., 1997). De Queiroz & Gauthier (1992) proposed three ways of defining higher taxon names phylogenetically [as ammended by Schander & Thollesson (1995), for the definition of taxon AB as implied by the phylogeny (C, (A,B))]: 1) stem-based definitions, where taxon names are defined as the most inclusive clade that contains taxon A but not taxon C; 2) node-based definitions, where taxon names are defined as the least inclusive clade that contains taxa A and B; and 3) apomorphy-based definitions where taxon names are defined as the most inclusive clade containing some synapomorphy of AB.

Biological classifications are built over categories created over 200 years ago by Linnaeus (1758). Evolutionary ranking adds retrievable information content to the classification, and is thus necessary, but Linnean categories are based on the essentialistic logic of Aristotelis, where ranks are absolutely arbitrary, with no implied meaning across distinct taxonomic groupings (de Queiroz & Gauthier, 1992; Christoffersen, 1995). Is there any sense in comparing an Order of Demospongiae with one such taxon of the Polychaeta? Taxa placed at the same categorical level do not represent equivalent entities (Sundberg & Pleijel, 1994). The Linnean hierarchy has proved a constraint where diversity is considerable, hence the need for a super-subtribe, for instance. Linnean categories add no stability to the names of taxa as changes in rank imply changes in suffixes (at least). It promotes redundancy via mandatory categories and the principle of exhaustive subsidiary taxa (e.g. Cantino et al., 1997). Biological classification might benefit from a change in paradigm.

Given the above rationale, phylogenetic classificatory schemes are proposed for the mycalid phylogeny where evolutionary hierarchy is preserved (retrievable) following some guidelines revised in Amorim (1997). In two of these the Linnean ranking is preserved. In the last proposed classification Linnean ranking is abandoned altogether.

MATERIALS AND METHODS

Specimens were studied under light and scanning electron microscopy. Preparations of thick sections and dissociated spicules were made using procedures described elsewhere (Hooper, 1991, 1997; Hajdu, 1994). Spicule measurements are given as minimum - *mean* - maximum dimensions in micrometres. SEM study was partly

performed in a Jeol JSM 35-L machine, under an accelerating voltage of 25KV, working distance of 15mm, and magnifications of up to 3600x; partly in a ZEISS DSM-940 machine, under accelerating voltages between 17 and 19KV, working distance around 8mm, and magnifications up to 10000x.

Phylogenetic analyses were performed using PAUP 3.1.1 (Swofford, 1993) with a choice for the ACCTRAN algorithm. Characters were treated as unordered and equally weighted on a first run. Subsequent weighting was applied on the basis of character's rescaled consistency indices. The phylogenetic classificatory schemes proposed are based on the guidelines revised by Amorim (1997). The four basic rules are: 1) every taxon must be monophyletic, or alternatively, if doubt persist, it must be stated clearly; 2) all the known levels of generality must be recognisable from the classification; 3) sister-group relationships must be recognisable; and 4) it must be possible to know to which larger clade a smaller clade pertains.

Nelson (1972) identified two ways of assigning less general clades to more general ones: subordination and 'sequenciation'. In subordinated classifications sister taxa share the same taxonomic category, and less inclusive clades are always associated to lower ranks than the more universal clades. In sequenced classifications, sister taxa need not share the same rank, but rather, successive lateral branches are associated to the same rank. Subordination has thus the advantage of naming every clade, what may turn into a disadvantage if there are more known levels of generality than taxonomic categories are available (but see Farris, 1976). Still, the finding of additional levels of generality (i.e. the inclusion of new taxa in the phylogeny) implies in considerable rearrangement of categories in a subordinated system. A more basic idea concerns the use of indentation to reflect distinct levels of universality (Wiley, 1979), a strategy adopted below.

In the alternative phylogenetic classifications proposed, no clade is given a new name due to the preliminarity of the exercise undertaken. In the classifications furnished below no choice was made for either subordination or 'sequenciation', as no new name is advanced and no Linnean category changed. Some procedures suggested by Wiley (1979), Amorim (1982, 1994), Christoffersen (1988) and Papavero et al. (1992),

TABLE 1. Rules adopted for the build-up of phylogenetic classifications from phylogenies, and their reference sources.

References	Rules
Wiley (1979)	'sedis mutabilis' for taxa pertaining to politomies
Amorim (1982)	'group+' for the more inclusive unnamed clade, which includes a less inclusive named group and its sister-group. 'group++' for the more inclusive unnamed clade, which includes a less inclusive 'group+' and its sister-group.
Christoffersen (1988)	'[taxon X]' for the lower rank taxon of a monotypic redundant higher rank one, where intermediary categories are simply ommited
Papavero et al. (1992)	'group-1, -2, -3, ...' - clades receive the names of their oldest included genus or species (every other rank is abandoned), to which a negative index is added to indicate the number of speciation events occurred between it and the actual taxon
Amorim (1994)	'group*' for the more inclusive unnamed clade, which includes a less inclusive named group pertainig to a polytomy, and its sister-group

were used in the construction of the classifications advanced below (see Table 1).

Abbreviations: BMNH, The Natural History Museum, London; INV-POR, Instituto de Investigaciones Marinas de Punta de Betin, Santa Marta, Colombia - Porifera collection; MNHN-LBIM, Muséum National d'Histoire Naturelle, Paris, Laboratoire de Biologie des Invertébrés Marins et Malacologie; MNRJ, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro; SMF, Senckenberg Museum, Frankfurt; UERJ, Universidade do Estado do Rio de Janeiro, Rio de Janeiro; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C.; USP, Universidade de São Paulo, São Paulo; ZMA, Zoologisch Museum Amsterdam, Amsterdam; ZMH-S, Zoölogisch Museum Hamburg, Schwam/Sponge collection.

SYSTEMATICS

Class **Demospongiae** Sollas
Order **Poecilosclerida** Topsent
Suborder **Mycalina** Hajdu, Van Soest & Hooper
Family **Mycalidae** Lundbeck

Naviculina Gray, 1867

DIAGNOSIS. *Mycale* with an ectosomal skeleton composed of a reticulation of megasclere budles. Anisochelae include naviculichelae (complete or near fusion of both frontal alae, falx markedly expanded along the shaft, lateral alae of the head project backward and upward). Type species: *N. cliftoni* Gray, 1867 (by monotypy).

Naviculina cliftoni Gray, 1867
(Figs 1-2)

Hymedesmia sp.; Bowerbank, 1864: pl. 37, fig. 152.
Naviculina cliftoni Gray, 1867: 538; Hooper & Wiedenmayer, 1994: 293.

MATERIAL. HOLOTYPE: BMNH 1877.5.21.270: Freemantle, Western Australia (type slide). COMPARATIVE MATERIAL. HOLOTYPE of *Mycale diastrophochela* Lévi, 1969: MNHN LBIM DCL1447: Vema Seamount, SE Atlantic. HOLOTYPE of *Mycale cleistochela* Vacelet & Vasseur, 1971: MNHN LBIM DJV36: Tulear, Madagascar. SPECIMENS: *M. cleistochela* ssp. *flagellifer*: MNHN LBIM DJV35: det. J. Vacelet & P. Vasseur, Tulear, Madagascar. ZMA 8512: det. R.W.M. van Soest, Sumbawa, Indonesia. ZMA 8896, 8897, 8912, 8917: det. R.W.M. van Soest, Tarupa Kecil, Indonesia. ZMA 12660: det. R.W.M. van Soest, Mahé, Seychelles. HOLOTYPE of *Mycale obscura* (Carter, 1882): BMNH 1881.10.21.318: Torres Strait, Queensland. SPECIMENS: BMNH 1925.11.1.732: det. M.E.Shaw, Tasmania, Australia. SMF 1041: det. E. Hentschel, Aru, Indonesia. ZMA 1602: det. M. Burton, Indonesian 'Siboga' material. ZMH-S 1670: det. E. Hentschel, Sharks Bay, Western Australia. SPECIMENS of *Mycale* spp.: INV-POR 2198: det. S. Zea, Colombian Caribbean. USNM 34348: det. Mote Marine Lab., off Florida, Gulf of Mexico. USNM 41555: det. E. Hajdu, Florida, Gulf of Mexico. MNRJ 263, 362, 425, 773: det. E. Hajdu, São Sebastião, Brazil.

REDESCRIPTION OF *NAVICULINA* GRAY, 1867. One single thick-section slide preparation remains. It contains a perfectly preserved fragment of the specimen's surface peel, from which it is possible to gather the whole series of spicules in *Mycale*. This peel contains an ectosomal skeleton characterised by a neat reticulation of megasclere bundles (2-6 spicules across) or single megascleres, forming meshes which are mostly triangular (40x70-240x350μm across), and inside which pores are clearly visible (60μm across). Naviculichelae abound inside the
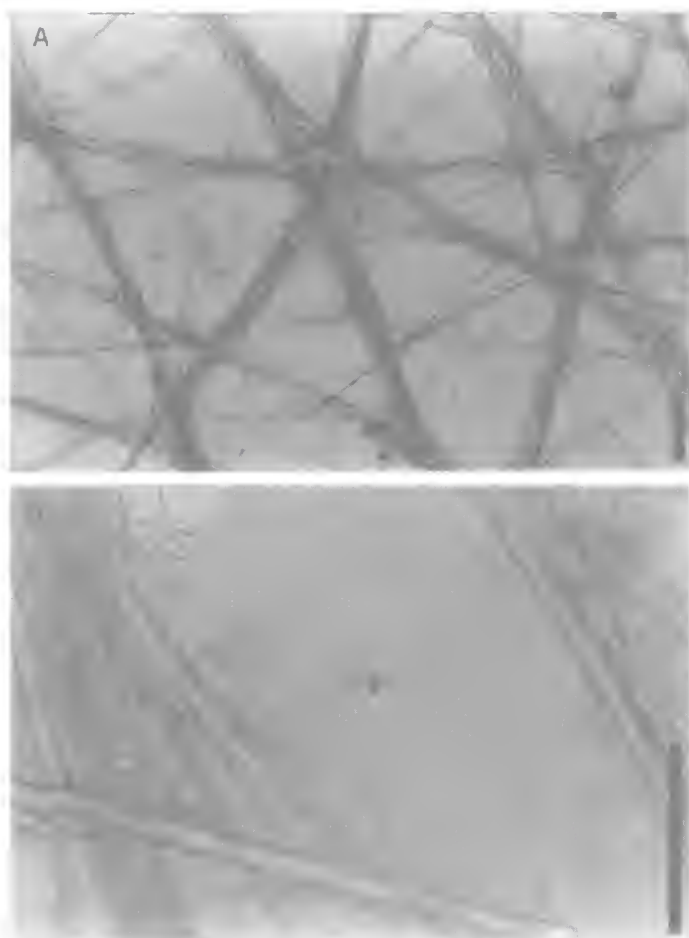
FIG. 1. *Mycale (Naviculina) cliftoni* (Gray, 1867). BMNH 1877.5.21.270. A, Neat ectosomal reticulation of megasclere bundles or single megascleres, most meshes triangular, pores clearly visible. Naviculichelae abound inside the meshes, specially around the bundles of megascleres. B, Mycalostyles, naviculichelae and a single sigma (arrow). Scale bars 100μm.

meshes, especially around the bundles of megascleres (Fig. 1A).

Spicules (light microscopy only, Fig. 1B). Megascleres: Mycalostyles, smooth, mostly straight, slightly fusiform, with elliptic or oval heads, and points which taper more-or-less gradually. Dimensions: 330-*357.4*-388μm long (N=20), 4.8-8.4μm thick (head, N=10), 6-9.6μm thick (shaft, N=10). Microscleres: Naviculichelae, head 60-70% the total spicule length, with narrowing and complete regression of the frontal alae of the head, which may touch the one of the foot, lateral alae of the head projecting backward and slightly upward,

downward expansion of the upper falx along the shaft. Dimensions: 12-*17.3*-21.6μm long (N=100). Sigma, slender, smooth, sharp endings. Dimensions: 14.4μm long (N=1).

REMARKS. The term naviculichela is proposed here for Bowerbank's (1864) "naviculiform spiculum". It is a type of anisocleistochela where there is complete or near fusion of both frontal alae (cf. Boury-Esnault & Rützler, 1997), the falx is markedly expanded along the shaft (Fig. 2A), and the lateral alae of the head project backward and upward (Fig. 2B) encircling the shaft. Another common feature is the extreme narrowing of the frontal ala, in such a way that it becomes thinner than the shaft itself (Fig. 2C). The term cleistochelae was first used by Topsent (1925) for the isochelae of a *Clathria*, a much simpler morphotype than that observed in *Naviculina cliftoni*, and related forms (e.g. *Mycale cleistochela* Vacelet & Vasseur, see below).

In *N. cliftoni* over 80% of the naviculichelae are 16.8-19.2μm long, and it is possible there are two categories [possibly 12-16.8 (N=15) and 18-21.6μm long (N=85)], but this is unclear from the distribution of spicule size categories. The origin of the single sigma observed is also dubious, possibly a contaminant.

DISCUSSION

A survey of nearly 230 published descriptions of *Mycale* revealed there were four species bearing naviculichelae-like anisochelae. These are: *M. cleistochela* Vacelet & Vasseur, 1971, *M. diastrophochela* Lévi, 1969, *M. obscura* (Carter, 1882), and *M. peculiaris* Pulitzer-Finali, 1997. However, the status of *M. cleistochela* ssp. *flagellifer* Vacelet & Vasseur, 1971 remains uncertain. It is possibly a separate species based on its distinctive microsclere complement, but a decision is not possible until detailed morphological comparisons are made of both taxa, which is beyond the scope of this present contribution.
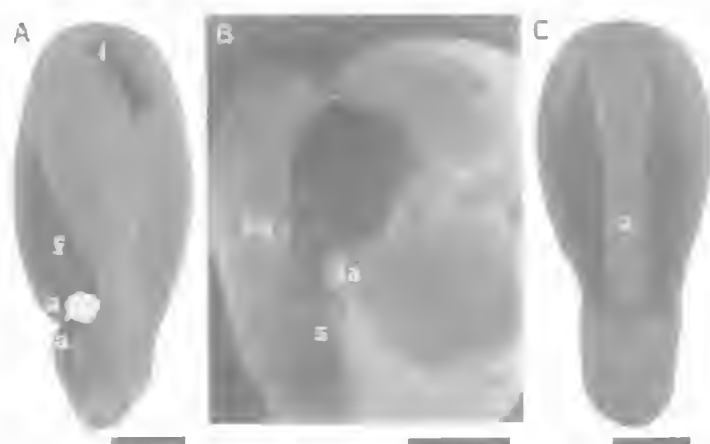
FIG. 2. A, Naviculichelae - anisochelae characterised by the complete or near fusion of both frontal alae (a). falx (f) markedly expanded along the shaft. B, Lateral alae (la) of the head projecting backward and upward, encircling the shaft (s). C, Extreme narrowing of the frontal ala (a), in such a way that it becomes thinner that the shaft itself. (A, C, MNRJ 773, *Mycale (Naviculina)* sp. B, USNM 41555, *Mycale (Naviculina)* sp. All scales bars 5μm.

All five taxa have neat ectosomal reticulations, potentially referable to *Mycale (Aegogropila)* (i.e. differentiated from other mycalids in having a neat ectosomal reticulation, but no serrated sigmas, and no isochelae). However, this act would be inconsistent with the use of *M. (Paresperella)*, for example, used for species with serrated-sigmas, to my knowledge, all bearing an ectosomal reticulation (Hajdu & Desqueyroux-Faúndez, 1994). A parallel can be made with the use of *M. (Grapelia)* for species with unguiferate anisochelae, all of which possess a confused tangential ectosomal architecture, typical of *M. (Mycale)* (Hajdu, 1995). Despite the fact that these names have been variably used as genera or subgenera in the past, it appears obvious that they comprise assemblages at distinct levels of universality. This is a common problem in the Linnean hierarchy, which has traditionally been ignored by the mere proposal of new scientific names for every assemblage recognisable on the basis of some more-or-less conspicuous trait; coupled to the acceptance of dustbin/plesiomorphic assemblages (i.e. *incertae sedis*).

PROPOSAL OF A FRAMEWORK FOR THE CLASSIFICATION OF THE MYCALIDS WITH ANISOCHELAE. The phylogenetic analysis of the Mycalidae undertaken by Hajdu & Desqueyroux-Faúndez (1994) has been reconsidered in light of the information derived from re-examination of *Mycale (Naviculina)*. Characters and taxa included in the analysis were reevaluated in view of decisions taken in Hajdu (1995). *Mycale (Anomomycale)*, *M. (M.) immitis*-group, *M. (Naviculina)*, *M. (Oxymycale)*, *M. (Rhaphidoteca)*, and *M. (Zygomycale)* have been added to the list of taxa considered here. *Esperiopsis*-I and -II were used as the outgroups, referring to those species conforming to *E. villosa* Carter, 1882 and *E. fucorum* (Esper, 1794), respectively. A list of 22 characters and their 50 states used in the cladistic analysis is given in Table 2. Taxa and their character states are tabulated in the datamatrix shown in Figure 3.

Figure 4 shows the preferred tree, selected with the purpose of advancing a discussion on phylogenetic classifications in mind (see below). It is a majority-rule consensus of 81 trees (50 steps. CI=0.94, RI=0.87, RC=0.82), filtered for more-resolved topologies from 1981 most parsimonious trees generated by PAUP's Branch and Bound exact algorithm for the datamatrix in Figure 3. Characters were treated as unordered, and multistate taxa were considered to be polymorphic. Following the suggestion by Nixon & Davis (1991), both *Mycale (Aegogropila)* and *M. (Carmia)* were split into terminal taxa -I and -II, to account for presence vs. absence of micracanthoxeas, respectively. In this way, the discussion advanced by Carballo & Hajdu (1998) on the status of micracanthoxeas within the mycalids can hopefully be refined. Ideally, this procedure would have been extended to every taxon polymorphic for one or more characters, but this would further reduce the resolution attained in Figure 4, through the addition of many more terminal taxa.

From this analysis neither *Mycale (Aegogropila)* nor *M. (Carmia)* are indicated as likely to be monophyletic. Carballo & Hajdu's (1998) hypotheses 2 and 4 appear more probable explanations for the observed distribution of micracanthoxeas. These hypotheses state, respectively, that either species that possess micracanthoxeas form a monophyletic clade, and one or both subgenera are polyphyletic; or poor taxonomic resolution (and/or interpretation)

TABLE 2. Morphological characters and their character-states used to build the datamatrix in Figure 3.

Characters	Character states
1. Categories of megascleres	0: one, 1: two or more rare, 2: two or more common
2. Main megascleres	0: (mycalo)styles only, 1: exotyles too; 2: oxeas only
3. Three categories of chelae	0: absent, 1: present
4. Basic shape of chelae	0: isochelae, 1: anisochelae
5. Rosettes	0: absent, 1: one category (maybe rare), 2: two categories maybe rare
6. Anisochelae-I with shaft markedly curved on profile view	0: absent, 1: present
7. Anisochelae-I ratio height of the head/total height of the spicule in %	0: > 35, 1: 25-35, 2: < 25
8. Anisochelae-I unguiferate	0: absent, 1: present
9. Anisochelae-I shape of the foot	0: normal (falx basal), 1: with pore (falx hidden within the alae), 2: contorted and denticulated
10. Anisochelae-II acanthose	0: absent, 1: present
11. Anisochelae-II	0: larger than III, 1: can be smaller than III
12. Anisochelae-II and/or III (naviculichelae) with falx extending downward along the shaft considerably	0: absent, 1: present
13. Anisochelae-II and/or III (naviculichelae) with frontal ala of the head extremely narrow (as thick as the falx itself)	0: absent, 1: present
14. Anisochelae-II and/or III (naviculichelae) with lateral alae of the head bent backward encircling the shaft	0: absent, 1: present
15. Anisochelae-III with a basal spur-like projection	0: absent, 1: present
16. Micracanthoxeas	0: absent, 1: present
17. Serrated sigmas	0: absent, 1: present
18. Toxas	0: absent, 1: present
19. Raphides	0: absent or one category, 1: maybe two categories
20. Ectosomal skeleton	0: absent, 1: reticulated; 2: confused
21. Choanosomal skeleton	0: absent, 1: stout quadrangular reticulation
22. Pore-grooves	0: absent, 1: present

prevents us from accessing the occurrence of micracanthoxeas in *M. (Aegogropila*-II*)* and *M. (Carmia*-II*)*, which would be monophyletic instead.

The strict consensus for the 81 trees selected holds the monophyly of (*Aegogropila*-I, *Carmia*-I) and of (*Anomomycale, Mycale (Grapelia, innitis*-group, *Rhaphidoteca*)). If we exclude the micracanthoxeas as potentially good synapomorphies, due to their largely underestimated occurrence, we are left with: 1) a confused tangential ectosomal skeleton, and 2) anisochelae-I markedly curved in profile view,

being the only real synapomorphies within the mycalids with anisochelae.

A posteriori weighting of characters in Figure 3 by their rescaled consistency indices does reduce the number of most parsimonious trees to 416 (36 after filtration), but this occurs at the expense of resolution. The majority-rule consensus is similar to Figure 4, but (*Oxymycale*), (*Naviculina, Paresperella, Zygomycale*), and ((*Aegogropila*-I, *Carmia*-I), *Carmia*-II) compose a polytomy next to the mycalids with a confused tangential ectosomal architecture.

It is interesting to note from the present analysis that the absence of an ectosomal skeleton in *Mycale (Carmia)* appears as a possible subsequent loss, as opposed to the findings reported by Hajdu & Desqueyroux-Faúndez (1994). As argued elsewhere (e.g. Hajdu & Van Soest, 1996), some losses are likely to be easily achieved, and conversely it could be expected that parallel developments might also have occurred. Hajdu & Rützler (1998) reported on a *M. (Aegogropila?)* which can have an ectosomal reticulation, or may lack any ectosomal skeleton whatsoever, thus supporting the hypothesis that such ectosomal architectures have a low adaptive value. In other words, a careful study of species currently assigned to *M. (Carmia)* may indicate a more appropriate allocation in several distinct monophyletic assemblages, related to assemblages bearing ectosomal specialisations. In these cases assemblages sharing the absence/loss of ectosomal specialisation would not form a monophyletic clade, as already foreseen by the inferred relationships between *Arenochalina* and *Carnia*.

PHYLOGENETIC CLASSIFICATION EXERCISES. Several proposals have been made in the specialist systematics literature, as to how a phylogenetic classification (i.e. one that reflects the relationships among taxa, should be

Taxa\Char.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Aegogropila	0	0	01	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	01	0	0
Anomomycale	2	0	0	1	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2	0	0
Arenochalina	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Carmia	0	0	01	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Grapelia	0	0	1	1	2	1	2	1	1	1	01	0	0	0	1	0	0	0	0	2	0	0
immitis-group	2	0	1	1	1	12	0	1	0	0	0	0	0	0	01	0	0	0	01	2	0	0
Mycale	2	0	01	1	1	0	0	0	0	0	0	0	0	0	01	0	0	0	01	2	0	01
Naviculina	0	0	01	1	1	0	0	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0
Oxymycale	0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Paresperella	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0
Rhaphidoteca	2	1	0	1	1	01	1	0	1	0	0	0	0	0	0	0	0	0	01	2	0	0
Zygomycale	0	0	1	01	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
Esperiopsis-I	0	0	01	0	01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Esperiopsis-II	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

FIG. 3. Datamatrix showing the 14 mycalid taxa and their character states, for 22 characters used in the phylogenetic analysis undertaken here. (Refer to Table 2 for a list of characters and character states).

constructed (e.g. Nelson, 1972; Griffiths, 1974; Wiley, 1979; de Queiroz & Gauthier, 1990, 1992; Papavero et al., 1992; Papavero & Llorente-Bousquets, 1993; Amorim, 1997). These classifications were proposed under the protocols of subordination and sequenciation, with a minor or major relation to Linnean categories. Both paleontologic, as well as biogeographic data have been variously included in several proposals, thus enhancing enormously the information content of classifications.

There are at least six distinct levels of universality (for clades inferred here to be monophyletic), for mycalids with anisochelae (Fig. 4). If the terminal taxa are considered species-groups, the next five hierarchic levels (each one successively more inclusive than the preceding), could be, for instance subgenera, genera, tribes, subfamilies and families. This is the outcome of extreme commitment to Linnean hierarchy in a subordinated system, where sister taxa are always assigned similar taxonomic rank (Nelson, 1972; Amorim, 1997). In such an arrangement, *Mycale* (mycalids with anisochelae), would be named a family instead. Every time a new clade is found through refining phylogenetic analyses, considerable changes would have to be implemented in the Linnean hierarchies. In an extreme situation, especially applicable for speciose groups, there might be more recognised hierarchic levels than Linnean categories. Farris (1976) proposed a series of prefixes (Super-, Hiper-, Mega-, Giga-, and Sub-, Infra-, Micro-, Pico-) to allow the establishment of a nearly infinite number of categories, but is this what we seek in a pragmatic systematics?

There are alternatives. Amorim (1982, 1994) suggested a coding strategy through which inclusive taxa (e.g. a 'potential family') would receive the name of their most basal taxon (e.g. a genus), coupled with a '+' to state that the 'potential family' includes the mentioned genus plus its sister-group. This occurs when relationships are resolved within the inclusive taxon, whereas if they are not, the chosen name would be that of the oldest taxon coupled to an '*'. Figure 5 shows the translation of the clado-gram in Figure 4 into one such classification, using the suggestion by Wiley (1979) regarding the labelling of taxa pertaining to politomies.

The advantages of this system are that phylogeny is retrievable, and changes in hierarchic levels need not reflect changes in Linnean categories, thus confering stability to names used day-by-day by non-specialists. Moreover, taxa may be kept at the hierarchic level to which they are currently assigned, and new names need not be established for every new clade. Instead, use is made of available names coupled to a symbol.

The disadvantage is not exclusive. The same Linnean category may have several distinct ontologic meanings (Fig. 5). What does a subgenus mean? Subgenera represent five distinct levels of generality in this classification. They are employed for the sake of stability only. However, suggestions were made in the past to confer ontologic meaning to Linnean categories.
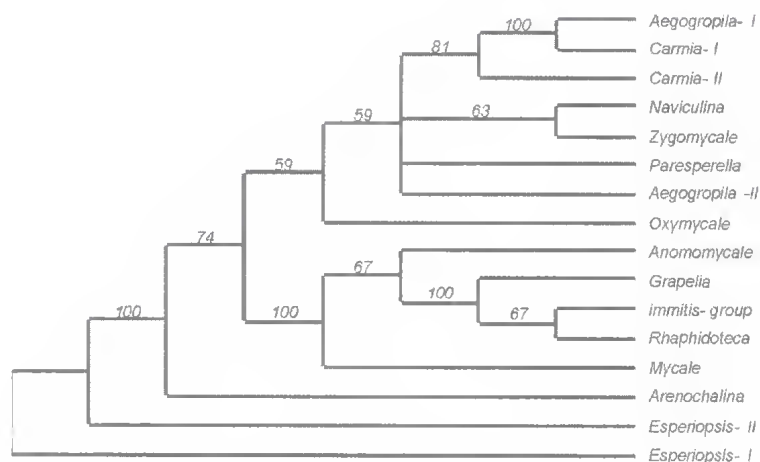
FIG. 4. Majority-rule consensus tree obtained from 81 trees filtered for more resolved topologies, and from 1981 most-parsimonious trees, showing the phylogenetic relationships of mycalids with anisochelae, obtained by analysing the datamatrix in Figure 3 using PAUP. Refer to Table 2 for a list of characters and states.

An alternative methodology is to look for biogeographic origin. According to Van Soest (1994), most demosponge higher taxa (suprageneric taxa) have notably wide distributions, an indication of their probable early ancestry (e.g. Van Soest & Hajdu, 1997). Knowledge of global tectonic events prior to the Triassic is fragmentary, so that no precise link would be possible between clades supposed to have originated before the break-up of Pangea and some likely original crustal plate. Additionally, Amorim (1997) stressed that any implementation of a classification in which clades are directly linked to biogeographic categories is clearly dependent on the elaboration of a well established general area cladogram.

These include an association between Linnean categories and a palaeontological age (e.g. Hennig, 1966), and the association of categories to their supposed biogeographic origin (Amorim, 1992). Unfortunately, neither source of evidence is readily available for the mycalids, or for that matter for most of the Poecilosclerida.

The oldest likely anisochelae-bearing mycalid (evidenced from a single palmate anisochela), is, to my knowledge, from the Early Cretaceous (Albian) (Wiedenmayer, 1994). This anisochela is only tentatively assigned to *Mycale*, and no finer allocation is possible. The next anisochela in the geologic scale is a curved, palmate form described by Gruber & Reitner (1991) (Lower Campanian, Cretaceous). This anisochela was assigned to a group within *Mycale*, the curved-assemblage of Hajdu (1995; as 'sp.2'). Its position in the cladogram (Hajdu, 1995, fig. 7.4) is more basal than both *M. (Grapelia)* and *M. (M.) immitis* species-group, but it is more derived in comparison to the remaining *M. (Mycale)*. In other words, there are subgenera of *Mycale* that are probably younger than the Campanian (ca. 80 Myr), and others that are probably older. Hajdu's (1995) 'sp. 3' is from the Eocene-Oligocene transition, thus younger than both records cited above, but sits in a more basal position in the cladogram. It is, therefore, pointless to assign geologic ages to categories within *Mycale*, on the basis of such a meager and patchy database.

Marine areas have been dealt with recently by many sponge specialists (Hooper & Lévi, 1994; Hajdu, 1995; Van Soest & Hajdu, 1997), and the general area cladograms generated would certainly form a framework over which to advance a classification along the lines suggested by Amorim (1992). Further speculation in this direction, however, is not possible until we draw a much clearer picture on the distribution of mycalids, as well as obtain well-supported cladograms for marine areas: all necessary prerequisites for the implementation of Amorim's (1992) suggestions.

For the time being, I propose a working hypothesis (Fig. 6), as a way of overcoming the problem of multiple significance of Linnean categories arrived at in Figure 5. This scheme takes into consideration the suggestion of Chiristoffersen (1988) on redundant taxa (Table 1), used here as an artifact to respect the hierarchic level of Linnean categories. The fundamental taxon is the genus *Mycale*. The terminal taxa are either subgenera or monophyletic species-groups, such as the *M. (M.) immitis*-group. Intermediate hierarchic levels are simply named 'groups', with their terminal taxa included within brackets, if monotypic.

Finally, a phylogenetic classification (Fig. 7), based on the cladogram in Figure 4, was built

Genus *Mycale* Gray, 1867

.....Subgenus *Arenochalina* Lendenfeld, 1887

.....group *Mycale*++

.........group *Mycale*+

..............Subgenus *Mycale*

..............group *Anomomycale*+ Topsent, 1924

...................Subgenus *Anomomycale*

...................group *Grapelia*+

.........................Subgenus *Grapelia*

........................group *Rhaphidoteca*+ Kent, 1870

.............................Subgenus *Rhaphidoteca*

.............................*Mycale immitis* (Schmidt, 1870) species-group

.........group *Oxymycale*+ Hentschel, 1929

..............Subgenus *Oxymycale*

..............group *Aegogropila*-II* Gray, 1867

...................Subgenus *Aegogropila*-II *s. m.*

...................Subgenus *Paresperella* Dendy, 1905 *s. m.*

...................group *Carmia*-II+ *s. m.*

.......................Subgenus *Carmia*-II

.......................group *Aegogropila*-I+

...........................Subgenus *Aegogropila*-I

...........................Subgenus *Carmia*-I

...................group *Naviculina*+ Gray, 1867 *s. m.*

.......................Subgenus *Naviculina*

.......................Subgenus *Zygomycale* Topsent, 1930

FIG. 5. Phylogenetic classification of the mycalids with anisochelae built from the cladogram in Figure 4, by subordination, incorporating the coding strategy of Wiley (1979), and Amorim (1982). Key: 'group+', more inclusive taxon containing the taxon formally described with that name (the basalmost taxon, preserving its current Linnean hierarchic status) and its sister-group; 'group*', more inclusive taxon (the oldest available name included), the relationships of its included taxa being unresolved. The priority of *Rhaphidoteca* Kent. 1870 over the *Mycale immitis* (Schmidt, 1870) species-group was decided not on the basis of knowledge of the actual dates of publication of both works, but on the fact that the species-group is bound to be named in the future, becoming then a much younger taxon: *s.m., sedis mutabilis*.

under the provocative protocol of Papavero et al. (1992) and Papavero & Llorente-Bousquets (1993), in which Linnean categories are simply abolished. Names considered are only those of genus- and/or species-level taxa, eventually coupled to an index which indicates their hierarchic level on the phylogeny.

For example, *Mycale immitis* (Schmidt, 1870) was used instead of *M. (M.) immitis*-group of Hajdu (1995). Its coupling to a '-5' index means that the supposed ancestor of the *M. (M.)*

immitis-group (the terminal taxon used in the present analysis), is 5 hypothetic ancestral species away from the true *M. immitis* species (Hajdu, 1995; fig. 7.4, 'species 10'). Thus, ancestor '-1' is the ancestor of *M. immitis* + its sister group ('species 6-9' of Hajdu, 1995); ancestor '-2' refers to 'species 1-10'; ancestor '-3' to 'species 1-12'; ancestor '-4' to 'species 1-16'; and, ancestor '-5' to the entire *M. (M.) immitis*-group (viz. 'species 1-17' of Hajdu, 1995).

Accordingly, *Mycale*₋₃ is the appropriate nomenclature in this case because *Mycale* is the oldest available name within the studied clade (page and line priority considered), coupled to the observation that the root of the clade containing all the mycalids with anisochelae is three ancestors away from the terminal *M. (Mycale)*. Ancestor '-1' is the ancestor of (*Myc*, (*Ano*, (*Gra*, (*Rha*, *imm*-group)))). Ancestor '-2' refers to the latter clade and its sister taxon, (*Aeg*-II, *Par*, (*Nav*, *Zyg*), ((*Aeg*-I, *Car*-I), *Car*-II)). And, ancestor '-3' to the whole ingroup.

PHYLOGENETIC DIAGNOSES FOR THE TERMINAL TAXA CONSIDERED. The cladogram in Figure 4 is a weakly supported working hypothesis. Accordingly, there are unnamed, more-inclusive clades remaining because relationships are bound to shuffle with the inclusion of additional terminal taxa. Nevertheless, this does not preclude the establishment of phylogenetic diagnoses for the taxa considered, as any phylogenetic hypothesis is better than no hypothesis at all. The cladogram (Fig. 4) is viewed as an improvement over the hypothesis put forward by Hajdu & Desqueyroux-Faúndez (1994) because it is a more comprehensive sample of probably monophyletic

Genus *Mycale* Gray, 1867

.....group *Arenochalina* [Subgenus *Arenochalina* Lendenfeld, 1887]

...group *Mycale*++

........group *Mycale*+

...........group *Mycale* [Subgenus *Mycale*]

. ...group *Anomomycale*+ Topsent, 1924

. ...group *Anomomycale* [Subgenus *Anomomycale*]

.................group *Grapelia*+ Gray, 1867

. ...group *Grapelia* [Subgenus *Grapelia*]

.....................group *Rhaphidotheca*+ Kent, 1870

..........................Subgenus *Rhaphidotheca*

............................*Mycale immutis* (Schmidt, 1870) species-group

........group *Oxymycale*+ Hentschel, 1929

.............group *Oxymycale* [Subgenus *Oxymycale*]

...........group *Aegogropila*-II* Gray, 1867

..................group *Aegogropila*-II [Subgenus *Aegogropila*-II] *s. m.*

.................group *Paresperella* Dendy, 1905 [Subgenus *Paresperella*] *s. m.*

...............group *Carmia*-II+ Gray, 1867 *s. m.*

......................group *Carmia* [Subgenus *Carmia*-II]

......................group *Aegogropila*-I+

....Subgenus *Aegogropila*-I

...........................Subgenus *Carmia*-I

....group *Naviculina*+ Gray, 1867 *s. m.*

.......................Subgenus *Naviculina*

.......................Subgenus *Zygomycale* Topsent, 1930

FIG. 6. Phylogenetic classification of the mycalids with anisochelae built from the cladogram in Figure 4, by subordination, incorporating the coding strategy of Wiley (1979), Amorim (1982) and a parallel of Christoffersen's (1988). Key: 'group+', more inclusive taxon containing the taxon formally described with that name (the basalmost taxon, preserving its current Linnean hierarchic status) and its sistergroup; 'group*', more inclusive taxon (the oldest available name included), the relationships of its included taxa being unresolved; *s.m., sedis mutabilis.*

species-groups within *Mycale* than the earlier attempt.

The proposed scheme is as follows:

Subgenus *Aegogropila*-I - *Mycale* with a reticulated tangential ectosomal skeleton and micracanthoxeas (many with toxas, and three categories of anisochelae).

Subgenus *Aegogropila*-II - *Mycale* with a reticulated tangential ectosomal skeleton (many with toxas, and three categories of anisochelae).

Subgenus *Anomomycale* - *Mycale* with a confused tangential ectosomal skeleton and anomochelae.

Subgenus *Arenochalina* - *Mycale* without any ectosomal skeletal specialisation, and with a stout choanosomal architecture composed of spiculofibres arranged in quadrangular meshes.

Subgenus *Carmia*-I - *Mycale* without any ectosomal skeletal specialisation and micracanthoxeas (many with toxas, and three categories of anisochelae).

Subgenus *Carmia*-II - *Mycale* without any ectosomal skeletal specialisation (many with toxas, and three categories of anisochelae).

Subgenus *Grapelia* - *Mycale* with a confused tangential ectosomal skeleton, three categories of anisochelae, anisochelae-I with a curved shaft in profile view, ratio height of the head/total height of the spicule < 25%, alae of the foot projecting downward forming a pore, and rosettes built both by anisochelae-I and -II (many with unguiferate anisochelae-I, acanthose anisochelae-II, and basally-spurred anisochelae-III).

Subgenus *Mycale* - *Mycale* with a confused tangential ectosomal skeleton (many with pore-grooves, three categories of anisochelae, basally-spurred anisochelae-III, and rhaphides in two categories).

Mycale (Mycale) immutis-group - *Mycale* with a confused tangential ectosomal skeleton, anisochelae-I with a curved shaft in profile view, ratio height of the head/total height of the spicule > 25% and < 35%, alae of the foot projecting downward forming a pore (many with pore-grooves, three categories of anisochelae, basally-spurred anisochelae-III, and rhaphides in two categories).

Subgenus *Naviculina* - *Mycale* with a reticulated tangential ectosomal skeleton, and naviculichelae (many with three categories of anisochelae, and toxas).

Subgenus *Oxymycale* - *Mycale* with a reticulated tangential ectosomal skeleton and megascleres which are oxeas exclusively.

Subgenus *Paresperella* - *Mycale* with a reticulated tangential ectosomal skeleton and serrated sigmas (many with toxas).

1. *Mycale*₃ Gray, 1867

2. *Mycale*₂ Gray, 1867; *Arenochalina* Lendenfeld, 1887

3. *Mycale*₁ Gray, 1867; *Aegogropila*-II₂ Gray, 1867

4. *Mycale* Gray, 1867; *Grapelia*₂ Gray, 1867

5. *Grapelia*₁ Gray, 1867; *Anomomycale* Topsent, 1924

6. *Grapelia* Gray, 1867; *Rhaphidoteca*₁ Kent, 1870

7. *Rhaphidoteca* Kent, 1870; *Mycale immitis*₅ (Schmidt, 1870)

8. *Aegogropila*-II₁ Gray, 1867; *Oxymycale* Hentschel, 1929

9. *Aegogropila*-II Gray, 1867; *Paresperella* Dendy, 1905; *Aegogropila*-I₂ Gray, 1867; *Naviculina*₁ Gray, 1867

10. *Aegogropila*-I₁ Gray, 1867; *Carmia*-II Gray, 1867

11. *Aegogropila*-I Gray, 1867; *Carmia*-I Gray, 1867

12. *Naviculina* Gray, 1867; *Zygomycale* Topsent, 1930

FIG. 7. Phylogenetic classification of the mycalids with anisochelae built from the cladogram in Figure 4 under the protocol of Papavero, Llorente-Bousquets & Abe (1992) and Papavero & Llorente-Bousquets (1993). Linnean categories are abolished, only genus- and species-level taxa are considered, hierarchy is retrievable from a numbered sequence attributed to the oldest taxon included (priority is applied to pages and lines also). The priority of *Rhaphidoteca* Kent, 1870 over *Mycale immitis*₅ (Schmidt, 1870) was decided not on the basis of knowledge of the actual dates of publication of both works, but on the fact that the species-group represented by *M. immitis*₅ is bound to be named in the future, becoming then a much younger taxon. (Refer to the text for further explanations).

Subgenus *Rhaphidoteca* - *Mycale* with a confused tangential ectosomal skeleton, exotyles. and anisochelae-I with alae of the foot projecting downward forming a pore (ratio height of the head/total height of the spicule may be > 25% and < 35%, rhaphides may be in two categories).

Subgenus *Zygomycale* - *Mycale* with a reticulated tangential ectosomal skeleton and isochelae next to anisochelae (many with three categories of anisochelae, and toxas).

Phylogenetic definitions for the above taxa based on apomorphies can be obtained by referring each clade to all the species sharing that clade's synapomorphies, and those of all its descendants. Apomorphy-based definitions have been severely criticised, however, because subsequent discovery of homoplasies can lead to substantial reshuffling of clades (e.g. Schander & Thollesson, 1995). The alternative option - using node-based definitions for the terminal taxa considered above - would be premature at this stage. The definition of more-inclusive taxa is dependent upon an unambiguous understanding of the less-inclusive taxa it contains. Cantino et al. (1997) chose to build their node-based definitions using only species level taxa, which were selected in such a way so that the more basal

genera included in the clade would be represented. These kind of data are absent, or nearly so, for most of the terminal taxa considered here. Where this information is available, node-based definitions can be powerful taxonomic tools (explicit, universal and stable). Hajdu (1995) published a phylogeny for the curved-assemblage of *Mycale*, which permits the derivation of node-based phylogenetic definitions for the *immitis*-group, *Rhaphidoteca* and *Grapelia*.

This scheme is as follows:

Subgenus *Grapelia* - the least inclusive clade that contains *Mycale myriasclera* Lévi & Lévi, 1983 and *Mycale burtoni* Hajdu, 1995.

Subgenus *Rhaphidoteca* - the least inclusive clade that contains *Mycale marshallhalli* (Kent, 1870) and *Mycale loricata* (Topsent, 1896).

Mycale (*Mycale*) *immitis*-group - the least inclusive clade that contains *Mycale trichela* Lévi, 1963 and *Mycale paschalis* Desqueyroux-Faúndez, 1990.

CONCLUSIONS

This discussion illustrates that current poriferan classifications may be very distant from truly phylogenetic schemes. While debate

persists on the merits and pitfalls of retaining the Linnean hierarchy, this does not excuse any proposal based on non-phylogenetic definitions for poriferan taxa. It is imperative that taxa are always diagnosed on the basis of their synapomorphies. This makes them more likely to be natural, and more relevant to future phylogenetic classification schemes. This is especially important when dealing with more-inclusive taxa, from which less-inclusive groups are extracted on the basis of their clearer mono-phyletic status. If, as is the current trend, effort is made toward defining such inclusive, plesiomorphic taxa (but excluding the extracted, less-inclusive taxa), it is likely that a paraphyletic assemblage will be recognised instead. In the phylogenetic system, groups such as these are going through a metaphorical 'mass-extinction episode' right now.

ACKNOWLEDGEMENTS

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PHOTOSYNTHESIS AND RESPIRATION OF THE CYANOBACTERIUM-CONTAINING SPONGE, *DYSIDEA HERBACEA*. *Memoirs of the Queensland Museum 44: 238. 1999*:- Marine sponges containing cyanobacterial endosymbionts are common in tropical waters, and the dictyoceratid sponge, *Dysidea herbacea*, is one of the most abundant sponges in the shallow lagoon at One Tree Reef, Great Barrier Reef. This sponge contains large numbers of the filamentous cyanobacterium, *Oscillatoria spongeliae*. The *O. spongeliae* trichomes are located free in the sponge mesohyl, although they are often in contact with archaeocytes. The high biomass of the cyanobacteria is illustrated by the chlorophyll *a* content of the association, which is about $335\mu g.mL^{-1}$ sponge volume, or $180.3\mu g.g^{-1}$ sponge wet weight. These values are much higher than for any other sponges so far studied.

Photosynthetic and dark respiration rates were measured using an oxygen electrode in summer and winter at ambient lagoon temperatures and at saturating irradiances. The compensation point for photosynthetic O_2 production is reached at about $30-50\mu mol$ photons.m^{-2}.sec^{-1} and photosynthesis saturates at about $300\mu mol$ photons.m^{-2}.sec^{-1}. No seasonal differences in the photosynthetic and respiration rates could be detected indicating that the sponge adapts to changing environmental conditions. The *D. herbacea/ O. spongeliae* association, does however respond to changes in temperature, with a Q_{10} for photosynthesis of about 5. Photosynthesis and respiration rates are also sensitive to the O_2 concentration in the seawater. The implications of these results for the ecology of this symbiotic association will be discussed. ☐ *Porifera, Dictyoceratida, cyanobacterium, symbiosis, photosynthesis, respiration, temperature.*

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